

RARITY IN THE CALIFORNIA FLORA: NEW THOUGHTS ON OLD IDEAS

PEGGY L. FIEDLER

Department of Biology,
San Francisco State University, San Francisco, CA 94132

ABSTRACT

Rarity in vascular plant species can be caused for a variety of reasons, such as old age or habitat specialization, and many of these causes have been discussed for over a century. Some of the more insightful ideas about the nature of rarity have sprung from California botanists intimate with the California flora. New thoughts that have expanded on older ideas about rarity suggest that, as a biological phenomenon in the California flora, it is a polythetic expression of several limiting factors, including, but not limited to age of origin, habitat specificity, and possibly a limited genetic diversity. While efforts to catalogue rare plants in California is increasing our understanding of their biology as well as their threats, little attention is paid to unprotected, but possibly unique populations of common as well as rare species. Such populations may represent the beginnings of the evolution of new rare plant forms. Less vigilance in the protection of these populations may result in a decelerating rate of evolution of new rare plant taxa in California.

Rarity is really a statement about geographic distribution and abundance (Drury 1974, 1980; Fiedler 1986; Fiedler and Ahouse 1992). As such, it represents at least three different phenomena. Rare species may be restricted in distribution, but abundant where found, as illustrated by the *Calochortus tiburonensis*. Other rare taxa may be more widespread, but never abundant where found. Sparsely distributed taxa, such as members of the genus *Nolina*, including the rare *N. interrata*, are excellent examples. Finally, rare taxa are often very localized and represented by only a few individuals. These rarities are rather few in number, e.g., *Lilium pardalinum* ssp. *pitkinense*, and typically are considered the most vulnerable to extinction due to habitat destruction.

California hosts an exceptionally large percentage of rare taxa, and much has been written about California's unique and famously rich flora (e.g., Raven and Axelrod 1978; Stebbins 1978a, b). It is generally accepted, for example, that the most famous of California's rarities are either old species—i.e., paleoendemics (e.g., *Sequoia sempervirens*, *Sequoiadendron gigantea*), or new species—neoendemics (e.g., *Linanthus killipii*, various members of the genus *Lasthenia*, and many other taxa). The California flora serves as an excellent backdrop to review the older ideas concerning the phenomenon of rarity, as the various causes of rarity can be illustrated clearly. I use

the term "old" broadly, in part because this review spans only a century's worth of research and synthesis, and in part because the newer ideas about the causes and consequences of rarity fall immediately on the heels of the older ones. My designation of old vs. new may seem arbitrary, but it suggests that we are now moving in new directions in the understanding, and ultimately, the preservation of California's rare plants.

HISTORICAL REVIEW: OLD IDEAS

I have divided the historical ideas about rarity into five broad categories. The categorizations are not necessarily complete, but are meant to represent the major ideas concerning rarity in vascular plants.

Age. Charles Lyell (1830–1833) and Charles Darwin (1872) believed that being rare was the precursor to becoming extinct. In short, they suggested that species that had persisted for a long, but unspecified length of time, were by definition rare, and thus were soon to become extinct. The American botanist Merritt Lyndon Fernald, most famous for his revision of *Gray's Manual of Botany*, later agreed with Darwin and Lyell (Fernald 1950). In a long series of papers on the flora of the eastern United States, Fernald developed a theory of relictual endemism citing age and consequently poor competitive ability as the reason for rarity in vascular plants (e.g., Fernald 1918, 1925, 1942).

Conversely, other botanists argued that rare taxa can be newly evolved. As early as 1836, in his publication *New Flora of North America*, Constantine Rafinesque suggested that old species were those with the most numerous individuals, and therefore new species must be those with the fewest individuals, and therefore rare. The correlation between geographic distribution and taxon age was fully articulated by J. C. Willis (1922) in his "Age and Area" hypothesis. Thus the discussion concerning whether rarities were old or new (but not both) was rather hotly debated for several decades in the early twentieth century (see e.g., Gleason 1924).

Ecology. In the mid-1800's, the British botanist H. C. Watson examined the phytogeography of rare plants in the British Isles and determined that the rare plants on this island group were habitat specialists. This autecological concept was echoed and further embellished by Herbert Mason for California's rare plants. In this regard, Mason published a pair of articles in *Madroño* (1946a, b) in which he pointed out that much of California's floristic diversity was the result of the superimposition of both diverse and unusual lithic features upon a wide range of climatic conditions.

Another major ecological theory concerning the cause of rarity

has to do with the competitive ability of plants. This was first fully articulated by Robert Griggs (1940), but demonstrated by Arthur Kruckeberg (1951) experimentally for certain taxa restricted to ultramafic substrates (e.g., *Streptanthus polygaloides*, *Achillea millefolium*) in his now classic competition experiments.

Genetics. The notion that rare species are genetically depauperate in some fashion was led by G. Ledyard Stebbins as early as 1942. He suggested that without either within population or among population allelic diversity, rare species could not respond to selective pressures that may cause them to wink out. Also in the early 1940's, Stanley Cain (1940) suggested that some rarities lacked an ability to colonize new habitats because of a low genetic heterozygosity and consequently narrow ecological amplitudes.

Later notions about rarity dealt with mutational loads—i.e., rare species are somehow less fit because they bear deleterious alleles (Wright 1956; Huxley 1963). Thus, geneticists of the Modern Synthesis argued that rare taxa are doomed because of unfavorable genetic scenarios.

Evolutionary events. Concepts of rarity regarding the evolution of localized taxa suggested that these species might evolve rather suddenly. Three major ideas put forth by Californian botanists are central here. Saltational speciation through catastrophic selection is based upon the premise that, in a variable and fluctuating climate, occasionally an extreme reduction of population size in marginal populations may be associated with reorganization of the gene pool (Lewis 1962). Harlan Lewis, most famous for his work on *Delphinium* and *Clarkia*, suggested that such drastic fluctuations are characteristic of populations of many annual plants in California. Several years later, Peter Raven (1964) linked catastrophic selection with edaphic endemism for various members of *Clarkia*, as well as for *Navarretia*, *Hesperolinon*, and the *Streptanthus glandulosa* complex.

A second evolutionary theme involves the likelihood of mutational events leading to a new breeding system. Les Gottlieb (1973a) documented the evolution of the new, rare taxon, *Stephanomeria malheurensis* from its parent species, *S. exigua* ssp. *coronaria*, by a single mutational change. The rare *Stephanomeria* is a self-pollinating species, while the common and widespread *Stephanomeria* is an obligate outcrosser.

Third, the now classic contribution by G. Ledyard Stebbins and Jack Major (1965) examined endemism and speciation in the California flora by identifying the evolution of endemic taxa through chromosomal rearrangement. They cite a wealth of examples, illustrating that chromosomal evolution via changes in ploidy level has had a major role in the evolution of California's rarities.

TABLE 1. OLD IDEAS CONCERNING RARITY IN VASCULAR PLANT SPECIES, WITH THE MOST CURRENT THINKING ABOUT EACH TOPIC SUMMARIZED.

I. Age

1. Rare species are "old" species (Lyell 1830-1833; Darwin 1872; Fernald 1918, 1925, 1929, 1942, 1950)
2. Rare species are "new" species (Rafinesque 1836; Willis 1922)

Current Synthesis: Rare species are of all ages. No broad generalizations about age of rarity can or should be made.

II. Ecology

1. Rare species are habitat specialists (Watson 1845)
2. Rare species are poor competitors (Griggs 1940; Kruckeberg 1951)
3. Rare species result from the superimposition of diverse and unusual lithic features upon a wide range of climatic conditions (Mason 1946a, b)

Current Synthesis:

1. Rare species can be habitat specialists, but many are not. No broad generalizations can or should be made.
2. Rare species can be poor competitors, such as in the genus *Streptanthus*, but many are not. No broad generalizations can or should be made.
3. A large proportion of the rare species in California do result from the superimposition of diverse and unusual lithic features upon a wide range of climatic conditions—a feature of the California flora recognized for over a century.

III. Genetics

1. Rare species exhibit low genetic diversity (Cain 1940)
2. Rare species consist of one or very few biotypes (Stebbins 1942)
3. Rare species resulted from the accidental fixation of deleterious (or useless) mutations (Wright 1956; Huxley 1963)

Current Synthesis:

1. Rare species can have low genetic diversity, but there are a number of exceptions, any of which come from the California flora. No broad generalizations can or should be made.
2. Rare species can consist of one of very few "biotypes," but no broad generalizations can or should be made. We have few data.
3. Rare species theoretically may have resulted from the accidental fixation of deleterious (or useless) mutations, but we have no empirical data to support this hypothesis.

IV. Evolutionary Events

1. Rare species originate from catastrophic selection on rare or unusual substrates (Raven 1964)
2. Rare species originate from a mutation leading to a new breeding system (Gottlieb 1973)
3. Rare (endemic) species originate through chromosomal rearrangement and the evolution of closely related taxa of different ploidy level (Stebbins and Major 1965)

Current Synthesis:

1. Rare species can originate from catastrophic selection on rare or unusual substrates, as in the genus *Clarkia*, but these data are hard to obtain. No broad generalizations can or should be made.
2. Rare species originate from a mutation leading to a new breeding system, as in the genus *Stephanomeria*, but these data are hard to obtain. No broad generalizations can or should be made.
3. Rare (endemic) species do originate through chromosomal rearrangement and

TABLE 1. CONTINUED

the evolution of closely related taxa of different ploidy level, and this was documented extensively by Stebbins and Major. However, this is not true in a universal sense, and no broad generalizations can or should be made.

V. Synthetic Approaches

1. Rare species are:

- (a) particularly susceptible to environmental stochasticities,
- (b) less competitive, and
- (c) less plastic in their ability to respond to new selection pressures (Darwin 1872)

Current Synthesis: True, but not in a universal sense. No broad generalizations can or should be made.

2. Rare species result from the interaction of:

- (a) a unique, localized environment,
- (b) a specific genetic structure of each population, and
- (c) a past evolutionary history peculiar to each taxon (Stebbins 1980: "Gene Pool-Niche Interaction Theory")

Current Synthesis: True, but not in a universal sense. No broad generalizations can or should be made.

Synthetic approaches. Darwin (1872) proposed that rare species are particularly susceptible to environmental stochasticities, less competitive, and less plastic in their ability to respond to new selection pressures (Darwin 1872). Although we cannot generalize as yet about multiple causes of rarity, his perspicacity presages our own, seemingly clumsy efforts to erect monothetic theories of cause.

One hundred years later, Stebbins (1980) put forth the gene pool/niche interaction theory, suggesting that rare species result from the interaction of a unique, localized environment, a specific genetic structure of each population, and a past evolutionary history peculiar to each taxon. The synthesis is very useful because we have come to realize that rare species are unlikely to be rare for any one single reason.

NEW IDEAS ABOUT RARITY

The new ideas about the causes of rarity presented below are really an update of what we think about these old ideas today. Table 1 summarizes the commentary below.

Age. In California, we have many old species or paleoendemics, probably the most famous are the redwoods *Sequoia sempervirens* and *Sequoiadendron giganteum*. From the fossil record we know that during middle Tertiary, the exceptionally rich mixed conifer

and subalpine forests of which these species were a part, shifted coastward as the cooling and drying trend accelerated (Raven and Axelrod 1978). Areas occupied by *Sequoia* and *Sequoiadendron* during the Tertiary were mutually exclusive as they are today. The more widely distributed genus *Sequoia* occurs farther north and coastward, inhabiting in a region of moister, milder climates. But there are other rare paleoendemics, such as *Lyonothamnus floribunda* and *Romneya coulteri*, with doubtless wider ranges in the Tertiary (Raven and Axelrod 1978). These taxa are now restricted to the relatively mild climates in California.

The age of other rare species is harder to ascertain, primarily because of an absence of rare plant fossils in the geologic record. Botanists must resort to correlative data, such as the geologic age of a specific habitat with the habitat specificity of a taxon. For example, Beal and Ownbey (1943) suggested that the rare triploid variety of *Calochortus longebarbatus*, *C. l.* var. *peckii*, endemic to the Ochoco Mountains of Central Oregon, is at least one million years old. These arguments were based on poor dispersal ability of the mariposa lily and the age of geological formation in which this mariposa lily is found.

New species, neoendemics, are represented by many examples in the California flora. It is generally accepted that most of California's endemics are new species (Stebbins 1978b). Most of these rarities are annual species, and are found in some more familiar genera, such as *Downingia*, *Eriogonum*, *Lasthenia*, *Limnanthes*, and *Linanthus*. *Eriogonum* is a particularly instructive genus. Skinner and Pavlik (1994) list 71 (approximately 36%) rare *Eriogonum* taxa in California, many of which are annual species.

Still other rare species may not be so old, or more importantly, their age is irrelevant in explaining causes of rarity. I suspect that many rare members of the Scrophulariaceae, such as *Castilleja affinis* ssp. *neglecta*, for example, are not particularly old or new. We simply lack evidence to invoke age as a reason for their limited distribution and abundance.

Ecology. What do we know about habitat specialists and about the competitive abilities of rare taxa? To answer the first question, we now know that many of our rarities in California are habitat specialists. This supports precisely what Herbert Mason suggested nearly fifty years ago—that California has a diversity in climate, topography, and soil type that is rivaled by almost nowhere else in the world. Although Mason (1946a, b) discussed at length our ultramafic endemic taxa, four additional examples illustrate the complexity of this phenomenon.

Brodiaea pallida is found in one extended population on vernal streambeds on serpentinite substrates in one small area of Tulare

County. It is threatened with development, and with possibly hybridization with *B. elegans*, a more common and widespread species. Thus its habitat requirements include a specific seasonal moisture regime on a very specific soil type in a very specific climatic zone. *Lilaeopsis masonii* is restricted to the littoral zone (splash zone) of Sacramento-San Joaquin Delta and Napa River. Its elevational range is only a few feet, and its primary habitat can be described as the ephemeral and precarious Delta shoreline that is subject to daily inundation by tidal action.

Calochortus striatus is a rare lily restricted to the vernal moist springs and meadows of the Mojave Desert, and *Oenothera deltooides* ssp. *howellii* is known from only seven populations in the rare and remnant aeolian sand deposits along the western edge of the San Joaquin River. These latter two species occur on ancient, remnant habitats characteristic of a time now past.

The second major ecological theory for rare plant species suggests that they are poor competitors. An interesting California example is the rare *Raillardiopsis muirii*—a species that provides several lessons about rarity in the California flora. This taxon has an extraordinary biogeographic history, as it is widely disjunct between the Ventana Double Cone in the Santa Lucia Range, and in the southern Sierra Nevada from Fresno to Kern County. Although the southern Sierra Nevada populations are nearly restricted to the Kings and Kaweah River drainages, there are three significant outlying populations—Baker Point, Church Dome, and Owens Peak. Baldwin and Kyhos (1990) proposed that this modest composite is 5 million years old, and represents the ancestral sister group to the Hawaiian tarweeds—a modest dispersal event (for a self-incompatible species) of over 3500 km. In addition to being a habitat specialist of considerable antiquity, it has been suggested that *Raillardiopsis muirii* may also be a poor competitor, being restricted to rather bare granitic substrates because it cannot compete successfully elsewhere.

Genetics. The genetics of rare species is a controversial topic, possibly because no consensus exists about the level of heterozygosity that characterizes rare plant taxa. In a recent review Hamrick et al. (1991) documented that endemic species, as representatives of rare taxa, have less than half the genetic diversity of widespread species. Narrowly and regionally distributed species have intermediate values. These documented differences in genetic diversity between endemic and widespread species are due largely to differences in the proportion of gene loci that are polymorphic (Hamrick et al. 1991). In addition, widespread species have more alleles at polymorphic loci than do endemic species.

There are many famous rarities in the botanical world that have little or no detectable genetic variation, such as *Pedicularis furbishiae*

(Waller et al. 1987), *Howellia aquatilis* (Lesica et al. 1988), and *Oenothera organensis* (Levin et al. 1979). California examples are also often cited, such as *Clarkia franciscana* and *Pinus torreyana*. But California also leads in the number of documented exceptions to this rule, as measured by percentage of gene loci that are polymorphic. For example, *Pinus longaeva* shows moderate to high amounts of polymorphism (79%, Hiebert and Hamrick 1983), *Layia discoides* is highly polymorphic (19 of 21 gene loci surveyed; Gottlieb et al. 1985); as is *Limnanthes bakeri* (39% of loci are polymorphic, Kesseli and Jain 1984); and *Dedeckera eurekensis* (77–89% of loci are polymorphic, varies with population; Weins et al. 1989). Nearly fifteen years after Stebbins (1980:80) concluded that “there appears to be no recognizable correlation, either positive or negative, between the amount of genetic variation within populations of plant species and the rarity or commonness of the species as a whole,” we cannot prove otherwise.

Finally, Wright's (1956) suggestion that rare species carry a high genetic load may be borne out in the rare paleoendemic shrub *Dedeckera eurekensis*. Weins and his colleagues (1989) found that less than 0.5% of the seeds of *Dedeckera eurekensis* are fully viable, and they suggest that this ancient taxon persists as rare, multiple-locus heterotic genotypes that have a low reproductive potential because of an excessively high segregational genetic load.

Evolutionary events. The genus *Clarkia* has presented California's systematists, along with her geneticists and ecologists, a wealth of questions about the evolution of rare forms. As mentioned previously, saltational speciation through catastrophic selection was developed by Harlan Lewis, in large part to illustrate the evolution of rare species of *Clarkia*. Although originally described for the derivation of *Clarkia franciscana* from *C. rubicunda*, Gottlieb (1973b) has shown that the former species is probably not derived in as direct a fashion as originally conceived by Lewis. However, this evolutionary mode of origin is likely to be true for other species of *Clarkia*, including *C. exilis* (Vasek 1958), *C. springvillensis*, *C. temblorensis*, and *C. caliente* from the widespread parental species *C. unguiculata* (Vasek 1971; Lewis 1973). The rare *Clarkia* species appear to evolve in progressive adaptation to increasing aridity, and all are accompanied by aneuploid changes in chromosome number, allopolyploidy, and autogamy (see Raven and Axelrod 1978 for a concise discussion of *Clarkia* evolution).

Synthetic approaches. The most useful approaches to understanding rarity in vascular plants is clearly one that takes a pluralistic approach. Rarity is not a monothetic phenomenon, but usually the congruence of several events. Perhaps the most useful descriptive synthetic approach is the one proposed by Rabinowitz (1981) and

Geographic Range	Large		Small	
	Wide	Narrow	Wide	Narrow
Habitat Specificity	Widespread Taxa	Predictable Taxa	Unlikely Endemic Taxa	Endemic Taxa
Large, Dominant, Local Populations	Common Plants - <i>Allium validum</i>	<i>Calochortus striatus</i>	<i>Allium munzii</i>	<i>Calochortus tiburonensis</i>
Small, Non-dominant, Local populations	Sparse Plants - <i>Muilla coronata</i>	<i>Nolina interrata</i>	Non-Existent?	<i>Brodiaea pallida</i>

FIG. 1. Seven forms of rarity (Rabinowitz 1981), as illustrated by various members of the California Liliaceae.

her students and colleagues, whose work on rare/common differences has inspired many of us to organize our thoughts about consequences of rarity (Rabinowitz 1978; Rabinowitz et al. 1979, 1984, 1989; Rabinowitz and Rapp 1981). Rabinowitz suggested that there are seven forms of rarity, as defined by geographic distribution, population size, and habitat specificity (Rabinowitz 1981). Floras or even taxonomic groups (Fig. 1) can be organized to provide insight into the types of rarities in a geographic region or phylogenetic context.

With respect to the synthetic approaches suggested by Darwin (1872) and Stebbins (1980), we know that evolutionary history, genetics, and habitat preferences explain the distribution of many taxa, both rare and common. And while these represent only three of the many variables that may explain rarity, synthetic viewpoints do not necessarily lead to broad generalizations about the causes and consequences of rarity.

A LOOK TO THE FUTURE

Bruce Pavlik and his students and colleagues are leading the way in rare plant biology today. They are clearly taking a synthetic approach, working experimentally to determine the causes of rarity in the exceedingly rare borage, *Amsinckia grandiflora* (Pavlik 1991a, b, 1992, in press). Pavlik's work demonstrates that careful, indeed elegant, experimental design can lead to definitive results explaining a rare plant's status.

Comparing rare and common congeners. One of the more fruitful approaches to understanding rarity is through the comparison of a rare taxon with a closely related common congener (e.g., Primack 1980; Karron 1987a, b, 1989). As mentioned before, Rabinowitz's work (Rabinowitz 1978; Rabinowitz et al. 1979, 1984, 1989; Ra-

binowitz and Rapp 1981) is seminal in this regard, as is the informative, but generally overlooked review by Babbel and Selander (1974). Two studies discussed below illustrate the utility of a comparative approach.

Recently, the reproductive biology of *Amsinckia grandiflora* was compared to that of the widespread *A. menziesii* var. *intermedia* (Pantone et al. in press). *Amsinckia grandiflora* is known from only three natural populations while *A. menziesii* var. *intermedia* is a widespread, rather aggressive weed across the semiarid western U.S. Interestingly, *A. menziesii* var. *intermedia* is increasing its range as this species establishes successfully in Australia, Europe, New Zealand, and South Africa (Pantone et al. in press). The two *Amsinckia* taxa have similar physiologies, morphologies, and phenologies, but they differ rather dramatically in their breeding system. *Amsinckia grandiflora* is heterostylous with probable seed abortion in flowers pollinated by the same floral morph, while *A. menziesii* var. *intermedia* is homostylous and self-fertile.

In the study, Pantone et al. (in press) documented that the differences in reproductive biology of the rare and common species, as determined by various measures of seed and inflorescence production, suggest that the homostylous weedy congener has overcome the intrinsic limits on fecundity set by heterostyly in its rare congener. Thus the constraints of a very specific breeding system dictate the intrinsic cause of rarity in *Amsinckia grandiflora*, and further limits to the successful seedling establishment and reproduction of this rare annual borage are imposed by the exotic grass species now naturalized within *Amsinckia*'s grassland habitat (Pavlik 1991a, b, 1992).

A number of years ago I documented reproductive differences among populations of rare species, and between populations of rare and common species of *Calochortus* (Fiedler 1987). The common species, *C. albus*, was found to reproduce at a smaller bulb size, produce a greater mean number of flowers and fruits per individual, and exhibit a higher amount of vegetative reproduction, as compared to the rare species *C. obispoensis* and *C. tiburonensis*, but not to *C. pulchellus*. In addition, the reproductive efforts appeared "chaotic" in the technical sense (Vandermeer 1982), and therefore gave credence to the suggestion that the population dynamics of rare species are chaotic. Finally, the common species also had a greater probability of survival to reproductive maturity, thereby increasing its reproductive success relative to the rare congeners (Fiedler 1987). However, despite these autecological life history differences, all populations of both rare and common species appeared to be, at the very least, stable or increasing in numbers, using a Leslie matrix approach (Fiedler 1987). I concluded that it is difficult to generalize about the life history or population dynamics for a rare species within

a single genus, and this admission diminishes a broader generalization about the behavior of rare plants.

“Perhaps the most significant aspect of this work is the conclusion that rare species may be idiosyncratic, *i.e.*, each rare species exhibits a host of individual and populational differences that distinguish it not only from more common species, also from other rare congeners.” (Fiedler 1987:993).

Anthropogenic vs. natural rarities. The preceding discussion has focused on natural rarities, or those species that are rare due solely to their biology, evolutionary history, or both. Anthropogenic rarities, however, are species that may or may not be rare due to the biology or evolutionary history, but currently are rare because of the negative impact interactions with humans have had on their populations (Fiedler and Ahouse 1992). They are not wholly distinct categories, however, as anthropogenic rarities may also begin as natural ones.

We can look to the new California Native Plant Society Inventory of Rare and Endangered Vascular Plants of California (Skinner and Pavlik 1994) to determine the proportion of rare taxa that are largely considered anthropogenic rarities. In the last five years since the previous edition (Smith and Berg 1988), the editors identified an additional 313 new rare and endangered plants (Table 2). Skinner and Pavlik (1994) suggest four reasons why there is such a increase.

- (1) Taxonomic changes have identified new rarities (7%). This nomenclatural shuffling is to be expected, and we shall always have a small percentage of rarities appear as our floras are updated.
- (2) Rare plants have been overlooked in the past. Approximately 63% of the 182 newly listed taxa in the 5th edition were not listed in previous editions because they were overlooked. This is extraordinary, largely because of the long history of intensive botanical surveys in California and the western United States (Ertter 1995), and because of California's well-known efforts to conserve its rare flora.
- (3) Many new plants (15%) have been described in California. This is wonderful news, and gives us confidence that competent and still inquisitive botanists are still working on the complexities of California's flora.
- (4) More plants (32%) are becoming endangered as habitat loss and other threats accelerate. This is troublesome, particularly with the recent predictions of staggering population increases for California in the coming century. These are the anthropogenic rarities to which we must turn in our protection efforts.

TABLE 2. PERCENTAGE OF FOURTH EDITION TAXA ON EACH LIST COMPARED TO THE NUMBER AND PERCENTAGE OF NEW FIFTH EDITION TAXA ON EACH LIST (SOURCE: SKINNER, M. W., AND B. M. PAVLIK, 1994).

CNPS list	% 4th Edition	Taxa new to 5th Edition	% new taxa
1A. Presumed Extinct in California	3%	3	1%
1B. Rare or Endangered in California & Elsewhere	44%	136	43%
2. R/E in California, More Common Elsewhere	11%	82	26%
3. Need More Information	10%	12	4%
4. Plants of Limited Distribution	33%	80	26%
Total	100%	313	100%

I predict that we will be focusing our conservation efforts more on the last of these rarities—i.e., anthropogenic rarities. I suggest further that this phenomenon is problematic, because knowing that they are anthropogenic rarities (and not, for example, competitively constrained) will provide little predictive power for preventing their populations from becoming extinct. The idiosyncratic nature of the taxa will become increasingly clear. Although we can separate causes of rarity from their consequences, in the case of anthropogenic rarities we must start with basic research on their autecology, without much theoretical power to guide our initial efforts.

CONCLUSIONS

In some fortunate instances, such as at the Eureka dunes, Inyo County, rare plant taxa, such as *Swallenia alexandrae* and *Oenothera avita* ssp. *eurekensis*, are more threatened by human disturbance, pollinator availability, and climatic fluctuations than by any intrinsic life history characteristic (Pavlik and Barbour 1988). These rare plants are spectacular examples of the California flora that are relatively secure. Such instances are relatively rare.

More disturbing are examples like *Lasthenia maritima* and *L. minor*. The former species is a rare composite restricted to the sea-bird islands along the coast of the Pacific Northwest, while the latter species, *L. maritima*'s progenitor, is not listed as rare, but is rapidly becoming rarer because of habitat destruction and degradation. The formerly common species may be more likely to go extinct than the naturally rare neoendemic.

Finally, we should not focus all our conservation efforts on our designated rarities, but instead, focus also on the protection of the rarest of things—e.g., individual or populational expressions of rare color forms, unusual morphologies, and rare genetic events. If we

do not redirect some of our management efforts toward these rarities. I suspect that we will lose much of the evolutionary theatre of California's magnificent flora, and that the period of rapid evolution of the majority of our rare species will have seen the final curtain.

LITERATURE CITED

- BABEL, G. R. and R. K. SELANDER. 1974. Genetic variability in edaphically restricted and widespread plant species. *Evolution* 28:619-630.
- BALDWIN, B. G. and D. W. KYHOS. 1990. A systematic and biogeographic review of *Raillardiopsis* [*Raillardella*] *muirii* (Asteraceae: Madiinae), with special reference to a disjunct California Coast Range population. *Madroño* 37:43-54.
- BEAL, J. M. and M. OWNBEY. 1943. Cytological studies in relation to the classification of the genus *Calochortus*. III. *Botanical Gazette* 104:553-562.
- CAIN, S. A. 1940. Some observations on the concept of species senescence. *Ecology* 21:213-215.
- DARWIN, C. 1872. *On the origin of species*. 6th edition. Mentor, USA.
- DRURY, W. H. 1974. Rare species. *Biological Conservation* 6:162-169.
- . 1980. Rare species of plants. *Rhodora* 82:3-48.
- ERTTER, B. 1995. The changing face of California botany. *Madroño* 42(2):114-122.
- FERNALD, M. L. 1918. The geographic affinities of the vascular flora of New England, the Maritime Provinces, and Newfoundland. *American Journal of Botany* 5:219-247.
- . 1925. The persistence of plants in unglaciated areas of Boreal America. *Memoirs of the American Academy of Arts and Science* 15:239-342.
- . 1929. Some relationships of the floras of the Northern Hemisphere. *Proceedings of the International Congress of Plant Sciences* 2:1487-1507.
- . 1942. Misinterpretation of Atlantic coastal plain species. *Rhodora* 44:238-246.
- . 1950. *Gray's Manual of Botany*. Corrected printing, 1970. D. Van Nostrand Co., New York.
- FIEDLER, P. L. 1986. Concepts of rarity in vascular plant species, with special reference to the genus *Calochortus* Pursh (Liliaceae). *Taxon* 35:502-518.
- . 1987. Life history and population dynamics of rare and common mariposa lilies (*Calochortus* Pursh: Liliaceae). *Journal of Ecology* 75:977-995.
- and J. J. AHOUSE. 1992. Hierarchies of cause: toward an understanding of rarity in vascular plant species. Pp. 23-47 in P. L. Fiedler and S. K. Jain, (eds.), *Conservation biology: the theory and practice of nature conservation, preservation and management*. Chapman and Hall, New York.
- GLEASON, H. A. 1924. Age and area from the viewpoint of phytogeography. *American Journal of Botany* 4:541-546.
- GOTTLIEB, L. D. 1973a. Genetic differentiation, sympatric speciation, and the origin of a diploid species of *Stephanomeria*. *American Journal of Botany* 60:545-553.
- . 1973b. Enzyme differentiation and phylogeny in *Clarkia franciscana*, *C. rubicunda*, and *C. amoena*. *Evolution* 27:204-214.
- , S. I. WARWICK, and V. S. FORD. 1985. Morphological and electrophoretic divergence between *Layia discoides* and *L. glandulosa*. *Systematic Botany* 10: 484-495.
- GRIGGS, R. F. 1940. The ecology of rare plants. *Bulletin of the Torrey Botanical Club* 67:575-594.
- HAMRICK, J. L., M. J. W. GODT, D. A. MURAWSKI, and M. D. LOVELESS. 1991. Correlations between species traits and allozyme diversity: implications for conservation biology. Pp. 75-86 in D. A. Falk and K. E. Holzinger (eds.), *Genetics and conservation of rare plants*. Oxford University Press, New York.

- HIEBERT, R. D. and J. L. HAMRICK. 1983. Patterns and levels of genetic variation in Great Basin bristlecone pine, *Pinus longaeva*. *Evolution* 37:302-310.
- HUXLEY, J. 1963. *The modern synthesis*. George Allen and Unwin, London.
- KARRON, J. D. 1987a. A comparison of levels of genetic polymorphisms and self-compatibility in geographically restricted and widespread plant congeners. *Evolutionary Ecology* 1:47-58.
- . 1987b. The pollination ecology of co-occurring geographically restricted and widespread species of *Astragalus* (Fabaceae). *Biological Conservation* 39: 179-193.
- . 1989. Breeding systems and levels of inbreeding depression in geographically restricted and widespread species of *Astragalus* (Fabaceae). *American Journal of Botany* 76:331-340.
- KESSELI, R. V. and S. K. JAIN. 1984. New variation and biosystematic patterns detected by allozyme and morphological comparisons in *Limnanthes* sect. *Reflexae* (Limnanthaceae). *Plant Systematics and Evolution* 147:133-165.
- KRUCKEBERG, A. R. 1951. Intraspecific variability in the response of certain native plants to serpentine soil. *American Journal of Botany* 38:408-419.
- and D. RABINOWITZ. 1985. Biological aspects of endemism in higher plants. *Annual Review of Ecology and Systematics* 16:447-479.
- LESICA, P., F. W. ALLENDORF, R. F. LEARY, and D. E. BILDERBACK. 1988. Lack of genetic diversity within and among populations of an endangered plant, *Howellia aquatilis*. *Conservation Biology* 2:275-282.
- LEVIN, D. A., K. RITTER, and N. C. ELLSTRAND. 1979. Protein polymorphism in the narrow endemic *Oenothera organensis*. *Evolution* 33:524-542.
- LEWIS, H. 1962. Catastrophic selection as a factor in speciation. *Evolution* 16:257-271.
- . 1973. The origin of diploid neospecies in *Clarkia*. *Am. Nat.* 107:161-170.
- LYELL, C. 1830-1833. *Principles of geology*. 1st ed. Murray, London.
- MASON, H. L. 1946a. The edaphic factor in narrow endemism. I. The nature of environmental influences. *Madroño* 8:209-221.
- . 1946b. The edaphic factor in narrow endemism. II. The geographic occurrence of plants of highly restricted patterns. *Madroño* 8:241-257.
- PANTONE, D. J., B. M. PAVLIK, and R. B. KELLEY. In press. The reproductive attributes of an endangered plant as compared to a weedy congener. *Biological Conservation*.
- PAVLIK, B. M. 1991a. Management of reintroduced and natural populations of *Amsinckia grandiflora*. Report prepared for the Endangered Plant Program, California Department of Fish and Game, Sacramento, CA. June 1991, 18 p.
- . 1991b. Reintroduction of *Amsinckia grandiflora* to three sites across its historic range. Report prepared for the Endangered Plant Program, California Department of Fish and Game, Sacramento, CA. June 1991, 50 p.
- . 1992. Inching towards recovery: evaluating the performance of *Amsinckia grandiflora* populations under different management regimes. Report prepared for the Endangered Plant Program, California Department of Fish and Game, Sacramento, CA. September 1992, 39 p.
- . In press. A framework for defining and measuring success in rare plant reintroductions. In P. Olwell, D. Falk, and C. Miller (eds.), *Restoring diversity: is reintroduction an option for endangered plants*. Island Press, Washington, D.C.
- and M. G. BARBOUR. 1988. Demographic monitoring of endemic sand dune plants, Eureka Valley, California. *Biological Conservation* 46:217-242.
- PRIMACK, R. B. 1980. Phenotypic variation of rare and widespread species of *Plantago*. *Rhodora* 82:87-95.
- RABINOWITZ, D. 1978. Abundance and diaspore weight in rare and common prairie grasses. *Oecologia (Berl.)* 37:213-219.

- . 1981. Seven forms of rarity. Pp. 205–217 in H. Synge, (ed.), *The biological aspects of rare plant conservation*. John Wiley and Sons, New York.
- and J. K. RAPP. 1981. Dispersal abilities of seven sparse and common grasses from a Missouri prairie. *American Journal of Botany* 68:616–624.
- , B. K. BASSETT, and G. E. RENFRO. 1979. Abundance and neighborhood structure for sparse and common prairie grasses in a Missouri prairie. *American Journal of Botany* 66:867–869.
- , J. K. RAPP, and P. M. DILLON. 1984. Competitive abilities of sparse grass species: means of persistence or cause of abundance? *Ecology* 65:1144–1154.
- , ———, S. CAIRNS, and M. MAYER. 1989. The persistence of rare prairie grasses in Missouri: environmental variation buffered by reproductive output of sparse species. *American Naturalist* 134:525–544.
- RAFINESQUE, C. S. 1836. *New flora of North America*. Publisher unknown, Philadelphia.
- RAVEN, P. H. 1964. Catastrophic selection and edaphic endemism. *Evolution* 18: 336–338.
- and D. I. AXELROD. 1978. *Origins and relationships of the California flora*. University of California Publications in Botany 72:1–134.
- SKINNER, M. W. and B. M. PAVLIK (eds.). 1994. *Inventory of rare and endangered vascular plants of California*. California Native Plant Society Special Publication No. 1, 5th ed. California Native Plant Society, Sacramento.
- SMITH, J. P., JR. and K. BERG (eds.). 1988. *Inventory of rare and endangered vascular plants of California*. California Native Plant Society Special Publication No. 1, 4th ed. California Native Plant Society, Sacramento.
- STEBBINS, G. L. 1942. The genetic approach to problems of rare and endemic species. *Madroño* 6:241–272.
- . 1978a. Why are there so many rare plants in California? I. Environmental factors. *Fremontia* 5(4):6–10.
- . 1978b. Why are there so many rare plants in California? I. Youth and age of species. *Fremontia* 6(1):17–20.
- . 1980. Rarity of plants: A synthetic viewpoint. *Rhodora* 82:77–86.
- and J. MAJOR. 1965. Endemism and speciation in the California flora. *Ecological Monographs* 35:1–35.
- VANDERMEER, J. 1982. To be rare is to be chaotic. *Ecology* 63:1167–1168.
- VASEK, F. C. 1958. The relationship of *Clarkia exilis* to *Clarkia unguiculata*. *American Journal of Botany* 45:150–162.
- . 1971. Variation in marginal populations of *Clarkia*. *Evolution* 18:26–42.
- WALLER, D. M., D. M. O'MALLEY, and S. C. GAWLER. 1987. Genetic variation in the extreme endemic *Pedicularis furbishiae* (Scrophulariaceae). *Conservation Biology* 1:335–340.
- WEINS, D., D. L. NICKRENT, C. I. DAVERN, C. L. CALVINS, and N. J. VIVRETTE. 1989. Developmental failure and loss of reproductive capacity in the rare paleoendemic shrub *Dedeckera eurekensis*. *Nature* 338:65–67.
- WILLIS, J. C. 1922. *Age and area*. Cambridge University Press, Cambridge.
- WRIGHT, S. 1956. Modes of selection. *American Naturalist* 90:5–24.

(Received 11 Jul 1994; accepted 3 Feb 1995)